

SYSTEMATICS OF *NAMA* (HYDROPHYLLACEAE):
COMPARISON OF SEED MORPHOLOGY OF SECTS.
ARACHNOIDEA AND *CINERASCENTIA* WITH FIVE
SPECIES OF *ERIODICTYON* AND
TURRICULA PARRYI

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ABSTRACT

Nama lobbii and *N. rothrockii*, members of the monotypic sects *Arachnoidea* and *Cinerascenia*, respectively, are divergent elements in *Nama* and their relationships with the genus have been questioned. Alternative genera with which the two might be allied are *Eriodictyon*, traditionally allied with *Nama*, or possibly, *Turricula*, historically associated with both genera. Utilizing scanning electron microscopy, seeds from five distinctive species of *Eriodictyon*, *E. crassifolium* var. *denudatum*, *E. tomentosum*, *E. traskiae* subsp. *smithii*, *E. angustifolium* and *E. californicum*, *Turricula parryi* and the two *namas* were examined for implications resident in seed morphology that might bear on placement of *N. lobbii* and *N. rothrockii*. Seeds of the *namas* are distinct from both *Eriodictyon* and *Turricula*, while seeds of the latter taxa are quite similar. Seed morphology combined with other available evidence suggests that *N. lobbii* and *N. rothrockii* are distinct phyletic elements within the Hydrophyllaceae.

INTRODUCTION

Nama is the second largest genus in the Hydrophyllaceae, housing about 50 species ranging from short-lived annuals to robust subshrubs. Distributionally, species occur predominantly in western and southwestern United States and Mexico but three venture into South America and one is endemic to Hawaii. They occupy a variety of habitats ranging from arid, alkaline-gypseous flats in the central Chihuahuan Desert to more mesic, but seasonally dry slopes and higher elevations in the sierras of western North America and eastern Mexico.

As treated by Hitchcock (1933), the genus is structured of five sections; *Arachnoidea*, *Cinerascenia*, *Conanthus*, *Zonolacus* and *Nama* (as *Eunama*). Much the largest, sect. *Nama* comprises an extremely diverse group of

species unified by their entire leaves, styles that are free or connate less than half their length, a superior ovary, membranous, loculicidally dehiscent capsules and axillary, extra-axillary or terminal, one, two or few-flowered cymose inflorescences. Each of the smaller sections is separated from the largest by clearly distinctive features; sect. *Conanthus*, (3 sp.), houses dichotomously branched annuals with styles connate over half their length; sect. *Zonolacus*, (1 sp.), exhibits a half inferior ovary; sect. *Arachnoidea*, (1 sp.), produces cartilaginous, loculicidally and septicidally dehiscent capsules; sect. *Cinerascentia*, (1 sp.), displays crenate leaves and capitate inflorescences.

Species of sects. *Arachnoidea* and *Cinerascentia*, *Nama lobbii* Gray and *N. rothrockii* Gray, respectively, are critical elements in *Nama*. They are the most divergent namas, morphologically, and thus, set the limits of *Nama*. Moreover, it is through *N. lobbii* that the nearest relative of *Nama* has traditionally been identified as *Eriodictyon*, so the former taxon serves in positioning *Nama*, as well. However, a growing body of evidence portrays these taxa as more distant from *Nama* proper than was reckoned by Hitchcock (1933) and their inclusion in *Nama* lately has been questioned (Bacon 1984, 1974; Chance and Bacon 1984; Raven and Axelrod 1978). For, not only do they diverge from the bulk of *Nama* in gross morphology, they also diverge in seed morphology (Chance and Bacon 1984), chromosome number (Bacon 1984, Cave and Constance 1947, 1959; see Constance 1963, for summary) and flavonoid chemistry (Bacon, Fang and Mabry, in review). Thus, placement of *N. lobbii* and *N. rothrockii* appears seriously challenged and their positioning elsewhere must be considered. Since *N. lobbii* has been closely associated with *Eriodictyon*, traditionally, the latter taxon is a logical alternative genus with which the former species and, perhaps, *N. rothrockii* might be more closely allied. A second alternative is the monotypic *Turricula*, historically associated with both *Nama* and *Eriodictyon*. Since seed morphology has proven informative in suggesting relationships not previously evident, morphologically, in *Nama* (and other groups, see Chance and Bacon 1984, and references therein), it follows that comparison of seed morphology among these four taxa might provide insight relevant to positioning of *N. lobbii* and *N. rothrockii*. Therefore, we have examined seed morphology of the two species of *Nama*, five distinctive species of *Eriodictyon*, *E. crassifolium* Benth. var. *denudatum* Abrams, *E. tomentosum* Benth., *E. traskiae* Eastw. subsp. *smithii* Munz, *E. angustifolium* Nutt., *E. californicum* (H. & A.) Torr., and *Turricula parryi* (Gray) Macbr. We report herein results of that survey and implications as they bear on placement of *N. lobbii*, *N. rothrockii* and systematics of *Nama* proper.

MATERIALS AND METHODS

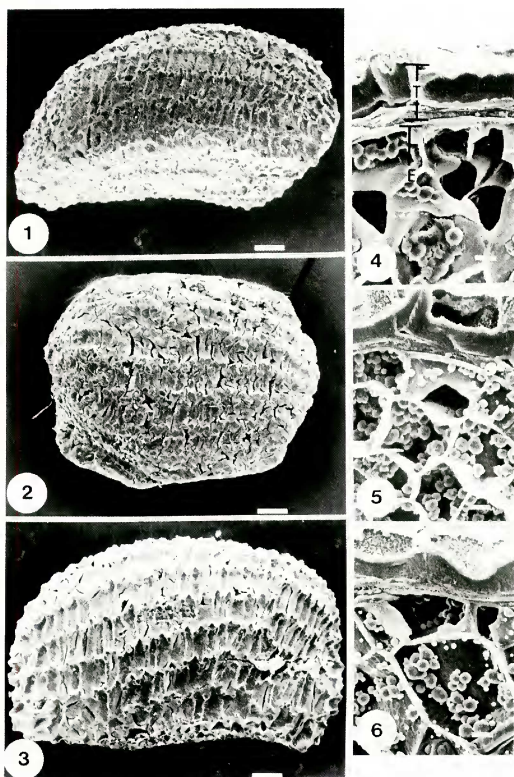
Mature, whole seeds removed from herbarium specimens were mounted on brass stubs with double-stick carpet tape. For examination of internal features of the testa, seeds were sectioned free-hand with a razor blade and mounted as for whole seeds. Specimens were coated to a thickness of approximately 25–30 nm in a Polaron E5100 sputter coater using gold-palladium target and examined with a JEOL JSM 35-C SEM at an accelerating voltage of 15 kV. A minimum of five seeds per collection was examined.

RESULTS

Seeds of examined species of *Eriodictyon* and *Turricula* are remarkably homogeneous. While there are variations in precise shape and size, as noted for seeds in other plant groups (see Chance and Bacon 1984, and references therein), generally, seeds of both taxa are irregularly oblong (Figs. 1,2,3,7,8,9) in outline, more or less angulate-wedge shaped in cross section and average over 1 mm in length (Table 1). The outer testa in all is clearly cellular in composition and surface patterning in all is shallowly reticulate, following the terminology of Chance and Bacon (1984). Reticulum cells are arranged into definite rows, with each cell elongated at right angles to the long axis of the seed. The longer radial walls in each cell are conspicuously concave. This organization accounts for their "transverse corrugations" as seen under the light microscope. In section (Figs. 4,5,6,10,11,12), the lower tangential wall of each reticulum cell appears weakly to strongly undulate suggesting thickenings or, perhaps, compres-

TABLE 1. Seed characteristics of *N. lobbiai*, *N. rothrockii*, *Eriodictyon* and *Turricula*.

Taxon	Length (\bar{X} ,mm)	Width (\bar{X} ,mm)	Coat Thickness (min-max, μ)
<i>N. lobbiai</i>	1.26	0.82	12–40
<i>N. rothrockii</i>	1.52	1.01	30–58
<i>E. angustifolium</i>	1.02	0.63	13–24
<i>E. crassifolium</i> var. <i>denudatum</i>	1.22	0.78	4–8
<i>E. tomentosum</i>	1.09	0.70	3–6
<i>E. trasketae</i> subsp. <i>smithii</i>			
Hannan 65	1.11	0.80	6–12
Hannan 60	1.29	0.71	10–12
<i>E. californicum</i>	1.03	0.62	6–8
<i>T. parryi</i>	1.10	0.70	10–16



Figs. 1-6. Seeds of *Eriodictyon*. (Bar in whole seed figures = 100 μ ; bar in section figures = 10 μ ; bars apply to all figures) 1. *E. crassifolium* var. *denudatum*, whole seed. 2. *E. tomentosum*, whole seed. 3. *E. smithii* subsp. *traskiae*, whole seed. 4. *E. crassifolium* var. *denudatum*, seed section (T = seed coat, E = endosperm, applies to all sections). 5. *E. tomentosum*, seed section. 6. *E. smithii* subsp. *traskiae*, seed section.

sion ridges. Radial walls, however, lack thickenings, with the possible exception of *E. tomentosum* (Fig. 5, upper left corner); however, additional examination is required to confirm or deny this possibility since potential thickenings do not occur in each reticulum cell in this species. The seed coat in these taxa varies in thickness among species and at different points within a single seed section (Table 1) and ranges from a low of 3μ in *E. tomentosum* to a high of 24μ in *E. angustifolium*.

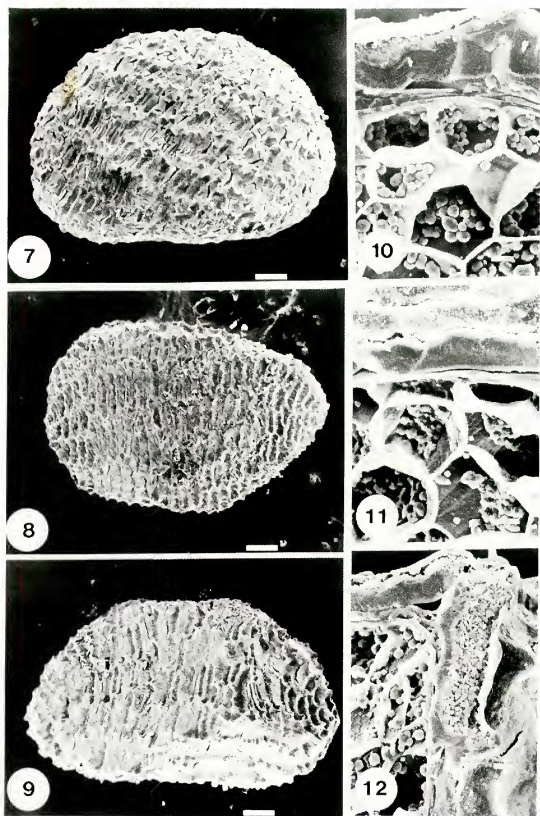
Seeds of *N. rothrockii* and *N. lobbii* (Figs. 13, 14) essentially conform with those as reported by Chance and Bacon (1984) except that seed coat thickness and average seed length of both is slightly less for seeds examined in this study. Seeds of the former taxon exhibit a foveolate-alveolate surface patterning and a solid outer testa $30\text{--}58\mu$ in thickness (Fig. 15; Table 1); those of the latter exhibit a papillose surface (Fig. 14) and a solid outer testa $12\text{--}40\mu$ in thickness (Fig. 16; Table 1).

Seeds of both *N. lobbii* and *N. rothrockii* are distinctive when compared with *Eriodictyon* or *Turricula*. Neither of the former species exhibits the chambered, ordered reticulum of the latter and the seed coat is generally much thicker in the former. In this last respect, however, the thinner areas in the testa of *N. lobbii* are within the range of variation in thickness of the testa in *Eriodictyon* and *Turricula*. Nevertheless, in overall morphology there is little similarity among seeds of *N. lobbii* or *N. rothrockii* and those of the latter genera.

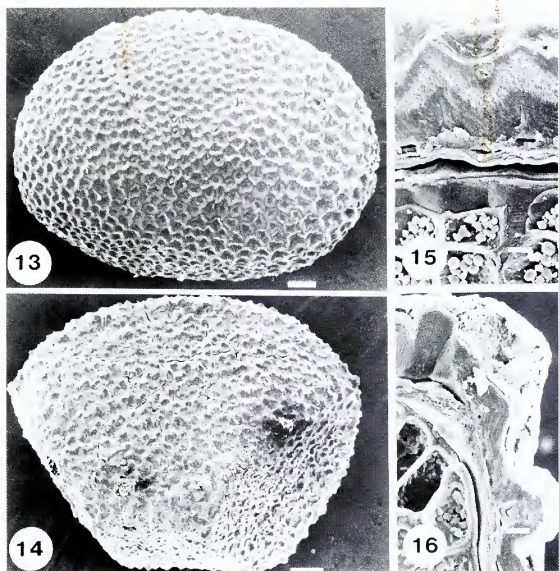
DISCUSSION

The lack of similarity in seed features of *N. lobbii*, *N. rothrockii* and *Eriodictyon* is accentuated by the striking similarity among seeds of the latter and *Turricula*; seed features clearly countenance an alliance of these two genera. However, neither of the names can be closely allied to *Eriodictyon* or *Turricula* based on seed characteristics, nor can they be closely allied one to another on these features. Indeed, seed morphology implies that both *N. lobbii* and *N. rothrockii* are elements phyletically distinct from *Eriodictyon*, *Turricula* and *Nama* (see Chance and Bacon 1984) and, therefore, distinct elements within the Hydrophyllaceae, as suggested by Bacon, Fang and Mabry (in review). Moreover, such a view is consistent with other available evidence and reconciles the lack of agreement in past dispositions of *N. lobbii*.

In structuring *Nama* into five sections, Hitchcock (1933) was recognizing the unique features exhibited by species forming the four smaller sections. Indeed, features of these species had long been appreciated, but there had been little agreement as to their systematic significance. Various workers had subjectively appraised one or another of these taxa as distinct



Figs. 7-12. Seeds of *Eriodictyon* and *Turricula*. 7. *E. angustifolium*, whole seed. 8. *E. californicum*, whole seed. 9. *T. parryi*, whole seed. 10. *E. angustifolium*, seed section. 11. *E. californicum*, seed section. 12. *T. parryi*, seed section.



Figs. 13–16. Seeds of *N. rotbrockii* and *N. lobbii*. 13. *N. rotbrockii*, whole seed. 14. *N. lobbii*, whole seed. 15. *N. rotbrockii*, seed section. 16. *N. lobbii*, seed section.

genera (e.g., Peter 1897, Gray 1875), as subgenera of *Nama* (Brand 1913, Jepson 1925) or as members of other recognized genera (Greene 1885, Hall 1906). In positioning *N. lobbii*, Hitchcock (1933) was aware that the taxon had been transferred to *Eriodictyon* by Greene (1885), accepted there by Hall (1906), but excluded from that genus in its then most recent treatment by Abrams and Smiley (1915). Entering into Hitchcock's (1933) deliberations, too, was the positioning of the problematical *Turricula*; originally described as a *Nama* (Gray 1880), the taxon was transferred to *Eriodictyon* by Greene (1889), where it was accepted by Hall (1902), but was rejected there by Abrams and Smiley (1915) and subsequently established as the monotypic *Turricula* by Macbride (1917). Hitchcock

concluded, nevertheless, that *T. parryi* was more appropriately housed in *Eriodictyon*; he retained *N. lobbii* as a section of *Nama* and then allied *Nama* and *Eriodictyon* through these two taxa.

Subsequent to Hitchcock's work, Cave and Constance (1942, 1944, 1947, 1950, 1959) and Constance (1963) have extensively surveyed chromosome numbers within Hydrophyllaceae. All species of *Eriodictyon* exhibit $n = 14$; *T. parryi* has $n = 13$, supporting its recognition as a monotypic genus. In contrast, *Nama*, including sects. *Conanthus* and *Zonolacus*, is strikingly diploid with $x = 7$ (only three species of *Nama* proper are consistently tetraploid; all are herbaceous and clearly to be related to other species in *Nama* proper; see Bacon 1984). However, *N. lobbii* exhibits $n = 14$, while *N. rothrockii* has $n = 17$ (Bacon 1974, 1984; Constance 1963), marking them as distinct within *Nama*. Chromosome number of *N. lobbii* supports its potential alliance with *Eriodictyon*; however, the number in *N. rothrockii* is known elsewhere in the family only in the South African *Codon*.

Chance and Bacon (1984) have found that seed morphology identifies six species groups within *Nama*. Species of sect. *Nama* compose five groups; importantly, species of sects. *Conanthus* and *Zonolacus* are separately accommodated in two of these five groupings. Species of sects. *Arachnoidea* and *Cinerascentia*, in contrast, form the sixth seed group; their seeds are much larger, exhibit a thicker seed coat and possess distinctive sculpturing patterns when compared with other groups. However, as evident herein, seeds of each taxon are distinctively organized, and Chance and Bacon (1984) noted that any relationship between the two should be viewed as distant with relationships to the bulk of *Nama* even more remote. Results presented in this report substantiate the views of Chance and Bacon (1984) and, furthermore, suggest that the two *namas* should be positioned some distance from both *Eriodictyon* and *Turricula*.

Flavonoid chemistry of *N. lobbii* and *N. rothrockii* has been determined (Bacon, Fang and Mabry, in review), and it is unique within *Nama*, as well; both taxa accumulate 6-oxygenated flavone aglycones, whereas other *namas* accumulate flavonoids with usual oxygenation patterns. However, flavonoids of three species of *Eriodictyon*, *E. tomentosum*, *E. californicum* and *E. angustifolium*, also have been resolved (Bacon et al., in review), and all accumulate 6-oxygenated flavone aglycones; chemistry of the two *namas* and three *eriodictyons* is quite similar, arguing that they are to be allied, nevertheless.

Morphologically, *Eriodictyon* is one of the more homogeneous genera of Hydrophyllaceae. All species are rhizomatous shrubs with scorpioid inflorescences, except for *E. capitatum* Eastw., and loculicidally and septicidally

dally dehiscent capsules (Munz and Keck 1959, Carlquist et al. 1983). As well, their uniform chromosome number and the uniformity in flavonoid chemistry and seed morphology among examined species argues convincingly that the genus represents a single phyletic element. To position *N. lobbii*, as suggested by Greene (1885), or *N. rothrockii* within *Eriodictyon* would destroy the homogeneity of the latter; although *N. lobbii* is woody and both names are rhizomatous (Bacon, pers. obs.; Jepson 1943), neither is a shrub, both tend to be spreading and mat-forming, and neither exhibits scorpioid inflorescences. Moreover, seed morphology of these taxa does not contenance such a union. Considering *Turricula*, its seed morphology clearly suggests a close alliance with *Eriodictyon*; however, while it possesses scorpioid inflorescences and its capsules dehisce in the same manner as do those of *Eriodictyon*, this perennial's upright, herbaceous habit and its chromosome number argue that it is correctly recognized. Seed morphology clearly distinguishes *N. lobbii*, in particular, and *Nama* proper, in general (see Chance and Bacon 1984), from *Turricula*. Therefore, any relationship between *Nama* and *Eriodictyon* is portrayed as less direct and more remote than surmised by Hitchcock (1933); in fact, how *Nama* proper relates to *N. lobbii*, *N. rothrockii* or *Eriodictyon* is not clear. Indeed, accumulated evidence suggests that *N. lobbii* and *N. rothrockii* are distinct phyletic elements within the Hydrophyllaceae. Their affinities, as suggested by their flavonoid chemistry and rhizomatous habit, lie nearer to *Eriodictyon* than to *Nama*, although *N. lobbii*, with its capsular dehiscence pattern, woody habit and chromosome number is nearer *Eriodictyon* than is *N. rothrockii*. Such a view renders *Nama*, although still diverse, more homogeneous and acknowledges the distinctive characteristics of *N. lobbii* and *N. rothrockii*. A treatment formalizing this view is forthcoming.

ACKNOWLEDGEMENTS

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APPENDIX: Source of Seed Samples

Vouchers for *Eriodictyon* are deposited at EMC;
those for *Nama* will be deposited at TEX.

Nama lobbii: CALIFORNIA: Eldorado Co.: 14 mi N of South Lake Tahoe on Hwy 89, near Emerald Bay, Bacon 1700. *N. rothrockii*: CALIFORNIA: Inyo Co.: 1.9 mi below Onion Creek Campground, 10.1 mi W of Independence, Bacon 1699. *Eriodictyon angustifolium*: UTAH: Washington Co.: 1 mi S of Pintura, Hannan 503. *E. crassifolium* var. *denudatum*: CALIFORNIA: Ventura Co.: California Hwy 33, 20.4 mi N of jct with California Hwy 150, Hannan

64. *E. tomentosum*: CALIFORNIA: Kern Co.: Park Hill Rd, 3.7 mi S of California Hwy 58, *Hannan* 58. *E. smithii* ssp. *traskiae*: CALIFORNIA: Santa Barbara Co.: E Camino Cielo Road, 7 mi W of Gibraltar Road, *Hannan* 60; California Hwy 1, 2.8 mi N of Burton Mesa Rd., Purisima Hills near Lompoc. *Hannan* 65. *E. californicum*: CALIFORNIA: Calaveras Co.: Old Priest Grade (California Hwy 120) W of Chinese Camp, *Hannan* 57. *Turricula parryi*: CALIFORNIA: San Diego Co.: Pine Valley, *Rose* 35306 (MICH).

REFERENCES

- ABRAMS, L. R. and F. J. SMILEY. 1915. Taxonomy and distribution of *Eriodictyon*. Bot. Gaz. 60:115–133.
- BACON, J. D. 1984. Chromosome numbers and taxonomic notes in the genus *Nama* (Hydrophyllaceae). II. Sida 10:269–275.
- . 1974. Chromosome numbers and taxonomic notes in the genus *Nama* (Hydrophyllaceae). Brittonia 26:101–105.
- BRAND, A. 1913. Hydrophyllaceae. In: Engler, Pflanzenreich, IV, 25:1–210.
- CARLQUIST, S., V. M. ECKHART and D. C. MICHENER. 1983. Wood anatomy of Hydrophyllaceae. I. *Eriodictyon*. Aliso 10:397–412.
- CAVE, M. and L. CONSTANCE. 1942. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 18:205–216.
- . 1944. Chromosome numbers in the Hydrophyllaceae. II. Univ. Calif. Publ. Bot. 18:293–298.
- . 1947. Chromosome numbers in the Hydrophyllaceae. III. Univ. Calif. Publ. Bot. 18:449–465.
- . 1950. Chromosome numbers in the Hydrophyllaceae. IV. Univ. Calif. Publ. Bot. 23:363–382.
- . 1959. Chromosome numbers in the Hydrophyllaceae. V. Calif. Publ. Bot. 30:233–258.
- CHANCE, G. D. and J. D. BACON. 1984. Systematic implications of seed coat morphology in *Nama* (Hydrophyllaceae). Amer. J. Bot. 71:829–842.
- CONSTANCE, L. 1963. Chromosome number and classification in Hydrophyllaceae. Brittonia 15:273–285.
- GRAY, A. 1875. A conspectus of North American Hydrophyllaceae. Proc. Amer. Acad. Arts 10:312–332.
- . 1880. Botany of California. In: Geological survey of California, 1:1–628.
- GREENE, E. L. 1885. Studies in the botany of California and parts adjacent. Bull. Calif. Acad. Sci. 1:201–202.
- . 1889. New or noteworthy species. VI. Pittonia 2:13–24.
- HALL, H. M. 1902. A botanical survey of San Jacinto Mountains. Univ. Calif. Publ. Bot. 1:1–140.
- . 1906. Studies on Californian plants. II. Zoe 5:263–266.
- HITCHCOCK, C. L. 1933. A taxonomic study of the genus *Nama*. Amer. J. Bot. 26:415–430, 518–534.
- JEPSON, W. L. 1925. Hydrophyllaceae. In: A manual of the flowering plants of California. Univ. California Press. pp. 809–835.
- . 1943. Hydrophyllaceae. In: A flora of California. Univ. California Press. pp. 223–297.
- MACBRIDE, J. F. 1917. Notes on the Hydrophyllaceae and a few other North American spermatophytes. Contr. Gray Herb. 49:23–59.

- MUNZ, P. A. and D. A. KECK. 1959. Hydrophyllaceae. In: A California flora. pp. 515-550.
- PETER, A. 1897. Hydrophyllaceae. In: Engler and Prantl, Naturl. Pflanzenf. IV, 3a:54-71.
- RAVEN, P. H. and D. I. AXELROD. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72:1-134.